Euphytica (2010) 173:129–140
DOI 10.1007/s10681-010-0142-y

Inheritance of beta-carotene-associated mesocarp color and fruit maturity of melon (*Cucumis melo* L.)

H. E. Cuevas · J. E. Staub · P. W. Simon

Received: 2 August 2009 / Accepted: 26 January 2010 / Published online: 10 February 2010

Abstract Melon (*Cucumis melo* L.) fruit production in U.S. can be improved through the introgression of early fruit maturity (FM) and the enhancement of fruit color [i.e., quantity of β-carotene (QβC); orange mesocarp]. However, the genetics of FM and QβC have not been clearly defined in U.S. Western Shipping market class melons (USWS). Thus, a cross was made between the monoecious, early FM Chinese line 'Q 3-2-2' (non-carotene accumulating, white mesocarp) and the andromonecious, comparatively late FM USWS line 'Top Mark' (carotene accumulating; orange mesocarp) to determine the inheritance of FM and QβC in melon. Parents and derived cross-progenies (F_1, F_2, F_3, BC_1P_1, and BC_1P_2) were evaluated for FM and QβC at Hancock, Wisconsin over 2 years. Estimates of narrow-sense heritability (h^2_N) for QβC and FM as defined by F_1, F_2, and BC (by individuals) were 0.55 and 0.62, respectively, while estimates based on F_3 families were 0.68 and 0.57, respectively for these traits. Mesocarp color segregation (F_2 and BC_1P_2) fit a two gene recessive epistatic model, which in turn, interacts with other minor genes. Although the inheritance of QβC and FM is complex, introgression (e.g., by backcrossing) of early FM genes resident in Chinese germplasm into USWS market types is possible. Such introgression may lead to increased yield potential in USWS market types while retaining relatively high β-carotene fruit content (i.e., orange mesocarp), if stringent, multiple location and early generation family selection (F_{3-4}) is practiced for FM with concomitant selection for QβC.

Keywords Beta-carotene · Carotenoid · Exotic germplasm · Nutraceutical · Vitamin A

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Introduction

Melon (*Cucumis melo* L; $2n = 2x = 24$) is an economically important, cross-pollinated vegetable

species. It can be subdivided into seven horticultural groups (i.e., Flexuosus, Conomon, Cantalupensis, Inodorus, Chito, Dudaim, and Momordica), where numerous market class differences [e.g., Ogen, Galia, Charentais, and U.S. Western Shipping (USWS)] typify within-group genetic diversity (Pitrat 2008). Although melons are grown worldwide, Asia produces more than 71% of the total world tonnage (FAO 2004; Lebeda et al. 2007). The United States of America is the third most prolific melon producer (behind China and Turkey), where ~37,000 ha provides a $400 million (USD) return to its economy (N.A.S.S. 2005).

The inheritance of yield in melon is complex (Zalapa et al. 2006), and is associated with component traits including days to anthesis, primary branch number, fruit number, fruit weight per plant and average weight per fruit (Lippert and Hall 1982; Zalapa et al. 2008). Early pistillate flowering is positively correlated with early harvest yield ($r = 0.24$; Zalapa et al. 2007), and early maturing cultivars may improve marketability by increasing harvest number (i.e., more production cycles per year). Broad-sense heritability based on F_3 families (h^2_{BF}) for early pistillate flower production is moderately high (0.64) in melon, where additive genetic effects are important for trait expression (Zalapa et al. 2006 and 2008). It is likely that early flowering is conditioned by many (at least nine) genes which contribute, in the main, relatively small effects (Monforte et al. 2004). In contrast, the inheritance pattern of days to anthesis in muskmelon (Group Cantalupensis) is controlled by relatively few genes (Bohn and Davis 1957). In fact, a recent QTL analysis in Group Cantalupensis germplasm identified three QTL associated with fruit maturity (FM) [refers to the number of days from sowing to first mature fruit (IPGRI 2003)], which explained 63% of the observed phenotypic variation (Cuevas et al. 2009).

The nutritional value of melon is variable, and dependent upon the market class, genotype, and growing environment (Lester and Eischen 1995). Fruits of orange mesocarp (i.e. orange fleshed) market types (e.g., Group Cantalupensis), for instance, are a rich source of dietary carotenes (primarily β-carotene, which is a precursor of Vitamin A) (Kläui and Bauernfeind 1981; Gross 1987). Concentrations of β-carotene in fruit with an orange mesocarp can range from 9 to 18 ppm in mesocarp tissue (Navazio 1994). Fruit of market classes possessing a white or green mesocarp possess a comparatively lower β-carotene content (quantity), but are nevertheless a rich source of other phytonutrients important for human health (Mares-Perlman et al. 2002; Giovannucci 2002).

Even though genes for green (*gf*; Huges 1948) and white (*wf*; Imam et al. 1972) fruit mesocarp have been previously reported, the genetics of melon mesocarp color and the inheritance of carotenoid expression has not been clearly defined. Clayberg (1992) indicated that green and white mesocarp are recessive to orange, where *gf* and *wf* interact epistatically, such that *wf*+_/*gf*+_, and *wf*+_/*gfgf* genotypes produce fruit with an orange mesocarp, the genotype *wfwf*/*gf*+_ bears fruits having a white mesocarp, and the *wfwf*/*gfgf* genotype develops fruit that possess a green mesocarp.

A more recent melon fruit flesh color inheritance study confirmed, that green mesocarp color (*gf* gene) was simply inherited as a recessive trait in F_2 and doubled haploid lines (DHL) derived from a cross between the Korean accession 'Shongwan Charmi' PI 161375 (green mesocarp) and a 'Piel de Sapo' market type (white mesocarp) (Monforte et al. 2004). However, quantitative trait loci (QTL) analysis in the same cross identified three loci associated with orange mesocarp, whose varied allelic combinations could not explain the observed phenotypic variation. Moreover, the action of these loci could not be confirmed by Eduardo et al. (2008) during comparative analysis of nearly isogenic lines developed from same parents of the DHL population examined by Monforte et al. (2004). In contrast, Fukino et al. (2008) and Périn et al. (2002) observed single gene segregation for orange mesocarp in recombinant inbred lines (RIL) derived from AR 5 (orange mesocarp) × 'Harukei No 3' (green mesocarp), and PI 16375 (green mesocarp) and 'Véndrantais' (orange mesocarp), respectively. This simple segregation was presumed to be associated with the action of *wf* gene, which is located on linkage group (LG) IX. Recently, analysis of F_3 families derived from a cross between the Chinese line 'Q 3-2-2' (white mesocarp) and 'Top Mark' (orange mesocarp) identified three QTL associated with mesocarp color variation, while two were located in a region syntenic with the *wf* and *gf* genes (Cuevas et al. 2009). It is likely that at least four loci condition mesocarp color variation in melon fruit depending on market type.

Predictable and consistent gain from selection (ΔG) requires breeding methodologies that incorporate knowledge of trait genetics (i.e., variance components and heritabilities) (Bernardo 2002). Genetic component analysis of traits in advanced generation families [e.g., variance components analysis (VCA)] and generation means analysis (GMA) have proven effective for estimation of genetic parameters and environmental variances associated with quantitative traits (Cockerham 1986; Hallauer and Miranda 1988; Lande 1981; Mather and Jinks 1982). Therefore, we employed data obtained from previously developed F_3 families derived from a relatively wide melon cross [Conomon/Momordica (Chinese accession, group not defined) × Cantalupensis (USWS)] used to identify QTL associated with FM and mesocarp color (Cuevas et al. 2009) for analyses of variance components (VCA) for these traits. In addition, F_2 and BC_1 populations were developed from same parental germplasm and used in generation means analyses (GMA) to elucidate the genetics of FM and the inheritance (i.e., gene action) of mesocarp color. This information, in conjunction with previous QTL marker-trait associations (Cuevas et al. 2008, 2009; Paris et al. 2008; Zalapa et al. 2007) in USWS melon, is required for efficient development of early FM cultivars with high β-carotene content fruit.

Materials and methods

Plant material

Plant materials consisted of F_3 families derived from the Chinese line 'Q 3-2-2' (white mesocarp, early FM) and USWS line 'Top Mark' (orange mesocarp, late FM) melon type as described in Cuevas et al. 2009. Additionally, F_1 plants derived from parental germplasm were self-pollinated to produce F_2 individuals, and backcrossed to yield BC_1P_1 ($F_1 \times P_1$) and BC_1P_2 ($F_1 \times P_2$) progeny for examination.

Experimental design

F_3 families

Experimental design for F_3 families was as described in Cuevas et al. 2009.

F_2 and backcross progenies

The F_2 and backcross progenies (BC_1P_1 and BC_1P_2) were evaluated in a randomized complete block design in the summer of 2006 and 2007, employing similar condition as described for F_3 families (Cuevas et al. 2009). Each of three experimental blocks consisted of parental lines (one P_1 and P_2 per block), F_1 individuals (one per block), and at least 70 F_2 and 100 of each backcross progeny type depending on seed availability.

Data collection

Mesocarp color classification and β-carotene content

Mesocarp color classification and analysis of β-carotene is described in Cuevas et al. 2009. It consists of five mesocarp color groupings using the Royal Horticulture Society (RHS) mini-color chart 2005 (Fig. 1), and their correspondingly quantity of β-carotene (Qβ C) determined by reverse phase high-performance liquid chromatography (Table 1).

Fruit maturity

Fruit maturity of an entry was defined as described in Cuevas et al. 2009. It consists of six fruit maturity categories, which represent the six-week of harvesting period of both years (Table 2). Fruit of line 'Q 3-2-2' does not slip/abscise at maturity as those of 'Top Mark', and, thus, the maturity of fruit of progeny derived from these lines was determined by color change (dark green to light green or yellow) and/or if fruit slip/abscise from the peduncle.

Genetic analyses and parameter estimation

Genetic ratio analysis

Mesocarp color groupings of classified F_2 and BC_1P_2 individuals were analyzed by Chi-square (χ^2) tests for goodness of fit using SAS. The ratios evaluated were 9:3:4 and 1:1:2 (white: green: orange) for the F_2 and BC_1P_2 generation, respectively.

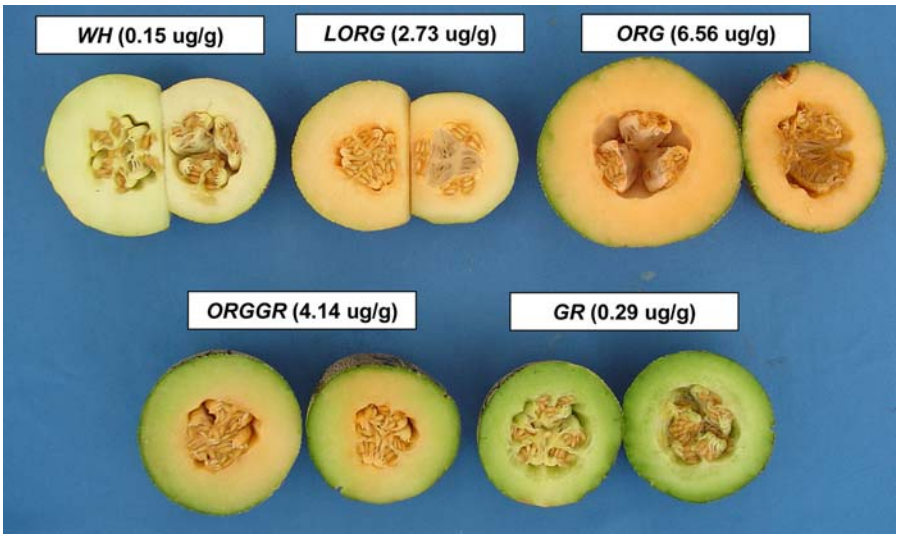

Fig. 1 Fruit mesocarp classifications and associated average β-carotene content (μg g^{-1}) in fresh weight used to characterized melon (*Cucumis melo* L.) parental lines, and segregating generations (F_2, BC_1P_1, BC_1P_2, and F_3 families) derived from a cross between Chinese line 'Q 3-2-2' (P_1) and 'Top Mark' (P_2) as evaluated at Hancock, Wisc. in 2006 and 2007 Color grouping according to the English Royal Horticultural Society (RHS) Mini-color Chart (2005). *WH* white mesocarp color (RHS-155B), *LORG* light orange mesocarp color (RHS-18C), *ORG* orange mesocarp color (RHS-23C), *ORGGR* orange-green mesocarp color (RHS-19B/RHS-149D), *GR* green mesocarp color (RHS-145B)

Table 1 Number of sample (n), means and high and low bounds of β-carotene content in fresh weight of melon (*Cucumis melo* L.) fruit mesocarp classifications used to characterize segregating generations (F_2, BC_1P_1, BC_1P_2, and F_3 families) derived from a cross of Chinese line 'Q 3-2-2' (P_1; white flesh) and 'Top Mark' (P_2; orange flesh) evaluated at Hancock, Wisc. in 2006 and 2007

Fruit mesocarp color[a]	n	β-carotene (μg g^{-1})		
		MEANS ± SE[b]	High	Low
Orange (*OR*)	16	6.62 ± 0.38 a	12.85	2.88
Orange-green (*ORGR*)	16	4.20 ± 0.60 b	6.27	2.22
Light orange (*LOR*)	8	2.36 ± 0.46 c	3.61	1.99
Green *(GR)*	20	0.25 ± 0.36 d	0.94	0.09
White (*WH*)	20	0.20 ± 0.36 d	0.38	0.06

[a] Color grouping according to the English Royal Horticultural Society (RHS) Mini-color Chart (2005). *ORG* orange mesocarp color (RHS-23C), *ORGGR* orange-green mesocarp color (RHS-19B/RHS-149D), *LORG* light orange mesocarp color (RHS-18C), *GR* green mesocarp color (RHS-145B) and *WH* white mesocarp color (RHS-155B or RHS-157B)

[b] *SE* standard error; estimators followed by the same letter are not significantly different at $P \leq 0.05$

Table 2 Fruit maturity rank utilized to characterized melon (*Cucumis melo* L.) parental lines, and segregating generations (F_2, BC_1P_1, BC_1P_2, and F_3 families) derived from a cross between Chinese line 'Q 3-2-2' (P_1) and 'Top Mark' (P_2) as evaluated at Hancock, Wisc. in 2006 and 2007

Fruit maturity rank[a]	Number of days within rank categories[b]	
	2006	2007
1	68–74	73–79
2	75–81	80–86
3	82–88	87–93
4	89–95	94–100
5	96–102	101–07
6	103–109	108–115

[a] Fruit maturity ranks correspond to the first through the sixth week of fruit harvest period

[b] Refers to days from transplanting to the development of the first mature fruit

Variance component analysis

The F_3 family data of Cuevas et al. (2009) were used to determine FM and QβC variance components (VCA). Expected genetic variance components were estimated according to Mather and Jinks (1982) as applied by Hallauer and Miranda (1988). The variation among F_3 progenies means (σ^2_{F3}) and its standard error (SE) were obtained for each trait directly from the *Proc mixed* output of SAS as the variance among F_3 family means. The mean variation of F_3 progenies ($\bar{\sigma}^2_{F3}$) was calculated by subtracting

the variance among plants (σ^2_{PP}) within homogenous entries (P_1, P_2, and F_1) from the plant-to-plant variation (σ^2_P). Estimates of additive variance (σ^2_A) and dominance variance (σ^2_D) were calculated as: $\sigma^2_A = [4\sigma^2_{\bar{F}3} - 2(\bar{\sigma}^2_{\bar{F}3})]/3$, and $\sigma^2_D = [8(\bar{\sigma}^2_{\bar{F}3}) - 4(\sigma^2_{\bar{F}3})]/3$. The approximate SE's for these genetic estimates were calculated using the following formulas derived from Hallauer and Miranda (1988): $SE(\sigma^2_A) = Sqrt[Var(\sigma^2_A)] = Sqrt\{[16Var(\sigma^2_{\bar{F}3}) + 4Var(\sigma^2_P) + 4Var(\sigma^2_{PP})]/9\}$, and $SE(\sigma^2_D) = Sqrt[Var(\sigma^2_D) = Sqrt\{[64 Var(\sigma^2_P) + 64Var(\sigma^2_{PP}) + 16Var(\sigma_{\bar{F}} 3^2)]/9\}$.

Generation means analysis

ANOVA was performed using *Proc mixed covtest method* Type 3 procedure of SAS and the β-carotene value of each individual. Year and generations were treated as fixed effects and blocks were considered as random effects. Best linear unbiased estimators (BLUEs) were estimated for P_1, P_2, and F_1, and best linear unbiased predictions (BLUPs) were estimated for F_2, BC_1P_1 and BC_1P_2 generation using the *Solution* option of the *model* statement of the *Proc mixed covtest* procedure. This procedure estimates fixed effects values from the raw data while making variable value adjustments during such estimations (de Leon et al. 2005).

The GMA for FM were conducted using a joint scaling test based on an additive-dominance model and sequential parameter model fitting (Mather and Jinks 1982). The joint scaling test [additive-dominance model; JNTSCALE software (Ng 1990)] was accomplished by weighting the means using the reciprocals of the variances of the generation means (wt_i = generation sample size/generation variance = n_i/S^2_i), where a failure of the model indicated the presence of epistasis. Additionally, a weighted scaling test method based on a six-parameter model [mid-parent, additive, dominance, homozygote × homozygote, homozygote × heterozygote and heterozygote × heterozygote interaction] was used according to Jinks and Jones (1958) and Mather and Jinks (1982) to determine what type of epistatic interaction was appropriate. The different parameter combinations were tested to identify a significance model using a χ^2 test in SAS.

The expected genetic variance components of each generation were estimated according to Mather and Jinks (1982). Estimates of environmental variance (σ^2_E), additive variance (σ^2_A), dominance variance (σ^2_D), and additive × dominance variance (σ^2_{AxD}) were calculated as: $\sigma^2_E = (¼\sigma^2_{P1} + ¼\sigma^2_{P2} + ½\sigma^2_{F1})$; $\sigma^2_A = 2(2\sigma^2_{F2} - \sigma^2_{BCP1} - \sigma^2_{BCP2})$; $\sigma^2_D = 4(\sigma^2_{BCP1} + \sigma^2_{BCP2} - \sigma^2_{F2} - ¼\sigma^2_{P1} - ¼\sigma^2_{P2} - ½\sigma^2_{F1})$, and $\sigma^2_{AxD} = \sigma^2_{BCP2} - \sigma^2_{BCP1}$. The standard error of each parameter was calculated as Sqrt{Var(V_x)}; where Var(V_x) is the variance of the parameter being examined. The Var(V_x) were estimated as $Var(V_x) = \sum[2[Var(k)]^2/(n + 2)]$; where Var($k$) represent each variance components present in the V_x (Lynch and Walsh 1998).

Heritability estimations

Broad- and narrow-sense heritabilities were estimated based on FM and QβC data obtained from GMA and VCA. In VCA, both heritabilities were estimated using the phenotypic variance of individual plants within F_3 families and variance of F_3 family means.

Estimation by GMA

Broad-sense heritability (h^2_B) was calculated as: $h^2_B = (\sigma^2_A + \sigma^2_D)/\sigma^2_P$; where σ^2_A, σ^2_D, and σ^2_P are the additive genetic variance, dominance genetic variance, and the phenotypic variance, respectively. The phenotypic variance was calculated as: $\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2_E$. Narrow-sense heritability was estimated as: $h^2_N = \sigma^2_A/\sigma^2_P$; where σ^2_A and σ^2_P are the additive genetic variance and the phenotypic variance, respectively. The standard error of these two parameters were calculated as: $SE(h^2_B) = [SE(\sigma^2_G)]/\sigma^2_P$; where $\sigma^2_G = \sigma^2_A + \sigma^2_D$, and the $SE(h^2_N) = [SE(\sigma^2_A)]/\sigma^2_P$ (Hallauer and Miranda 1988).

Estimation by VCA

Broad-sense heritabilities for FM and QβC based on phenotypic variance of individual plants within F_3 families (h^2_{BP}) were calculated as: $h^2_{BP} = (1/2\sigma^2_A + 1/2\sigma^2_D)/\sigma^2_P$; where σ^2_A, σ^2_D and σ^2_P are the additive genetic variance, dominance genetic variance and the phenotypic variance of individual plants within F_3 families, respectively. The phenotypic variance of individual plants within F_3 families (i.e., plant-to-plant variation) was obtained directly from the SAS output. The broad-sense heritabilities based on F_3 family means (h^2_{BF})

were calculated as: $h^2_{BF} = (1.0166\sigma^2_A + 0.266\sigma^2_D)/\sigma^2_{PF}$; where σ^2_A, σ^2_D, and σ^2_{PF} are the additive genetic variance, dominance genetic variance, and the phenotypic variance based in F_3 families means, respectively. Additive and dominance genetic variance were adjusted for family size using coefficients proposed by Kearsey and Pooni (1996). The SE of broad-sense heritabilities based on individual plants within F_3 families were calculated as: SE $(h^2_{BP}) = \{1/2[SE(\sigma^2_A)] + 1/2[SE(\sigma^2_D)]\}/\sigma^2_P$, and the SE of the broad-sense heritabilities based on F_3 family means was calculated as SE $(h^2_{BF}) = \{1.0166[SE(\sigma^2_A)] + 0.266[SE(\sigma^2_D)]\}/\sigma^2_{PF}$.

Narrow-sense heritabilities based on individual plants within F_3 families (h^2_{NP}) were estimated as: $h^2_{NP} = 1/2\ \sigma^2_A/\sigma^2_P$; where σ^2_A and σ^2_P are the additive variance and the phenotypic variance of individual plants within F_3 families, respectively. The narrow-sense heritabilities based on F_3 families (h^2_{NF}) were estimated as: $h^2_{NF} = 1.0166\sigma^2_A/\sigma^2_{PF}$; where σ^2_A and σ^2_{PF} are the additive variance and the phenotypic variance based on F_3 families, respectively. The phenotypic variance based on F_3 family means was estimated as: $\sigma^2_{PF} = (\sigma^2_P + p\sigma^2_{YxF} + bp\sigma^2_{F3})/bp$; where σ^2_P, p, σ^2_{YxF}, b, and σ^2_{F3} refer to plant-to-plant variation, number of plants per plot, variance due to year × family interaction, number of blocks, and variance among F_3 family means, respectively. The SE of the narrow-sense heritability on individual plants within F_3 families was calculate as: SE $(h^2_{NP}) = 1/2\ [SE(\sigma^2_A)]/(\sigma^2_P)$ and the SE of narrow-sense heritability based on F_3 family means was calculated as SE $(h^2_{NF}) = 1.0166[SE(\sigma^2_A)/\sigma^2_{PF}]$.

Estimation of the minimum number of effective factors

Since progeny distributions of F_3 families more adequately approximated normality than F_2 progeny (data not presented), the minimum numbers of effective factors were estimated via the variance value obtained from VCA. The minimum number of effective factors (n) influencing QβC and FM were estimated according to Castle (1921) and Wright (1968) using the correction factor suggested by Cockerham (1986) as: $n = [(\bar{P}_1 - \bar{P}_2)^2 - (\sigma^2_{\bar{P}1} + \sigma^2_{\bar{P}2})]/(8 \times \sigma^2_A)$; where $\bar{P}_1$ and $\bar{P}_2$ are the estimates of P_1 and P_2 parental means, $\sigma^2_{\bar{P}1}$ and $\sigma^2_{\bar{P}2}$, are the estimates of variance of the parental lines means, and σ^2_A is the additive genetic variance.

Phenotypic and genetic correlation

Phenotypic correlations between fruit QβC and FM in the F_2 and backcross progeny generations were calculated as Spearman coefficients using SAS. The genetic correlations and their attending standard errors were calculated according to Falconer and Mackay (1996).

Results

Analysis of variance

BLUE values of QβC and FM for parental lines and BLUP values for their derived advanced generations (F_2, BC_1P_1, and BC_1P_2) are presented in Table 3. The

Table 3 Best linear unbiased estimations and standard error (SE) for β-carotene content in fresh mesocarp tissue and fruit maturity of melon (*Cucumis melo* L.) Chinese line 'Q 3-2-2' (P_1), 'Top Mark' (P_2), and their F_1 progeny, and best linear unbiased predictions and SE for F_2, BC_1P_1 and BC_1P_2 population as evaluated in Hancock, Wisc. in 2006 and 2007

Generation	β-carotene (μg g^{-1}) ± SE[a]	Fruit maturity (rank) ± SE[b]
'Q 3-2-2'	0.68 ± 0.34	1.65 ± 0.29
'Top Mark'	5.78 ± 0.45	4.40 ± 0.37
F_1	0.71 ± 0.33	1.77 ± 0.29
F_2	1.47 ± 0.66	3.05 ± 0.54
BC_1P_1	0.48 ± 0.66	2.24 ± 0.54
BC_1P_2	2.66 ± 0.66	4.01 ± 0.54

[a] β-carotene content is based in the means value of five different fruit mesocarp color categories (orange = 6.62 μg g^{-1}; orange-green = 4.20 μg g^{-1}; light orange = 2.36 μg g^{-1}; green = 0.25 μg g^{-1}, and white = 0.20 μg g^{-1})

[b] Fruit maturity based on fruit maturity ranking (1–6), which refers to the 6 week harvesting period starting from the first mature fruit

F_1 generation performed similar to 'Q 3-2-2' for QβC and FM. The BLUP value of QβC for the BC_1P_2 and F_2 generations were lower than the mid-parent value, while BC_1P_1 and 'Q 3-2-2' values were identical. In contrast, while BLUP values of FM for the mid-parent and F_2 progeny were the same, BC_1P_1 and BC_1P_2 values were lower and higher, respectively, than the respective mid-parent value. Backcross and F_2 progeny values, however, did not approach upper or lower parental values for FM in each year.

Phenotypic segregation of mesocarp color

White mesocarp was dominant in this cross combination given that all fruit of F_1 and BC_1P_1 progeny possessed white mesocarp typical of the 'Q 3-2-2' parent (Table 4). In contrast, the mesocarp of fruit on F_2 or BC_1P_2 progeny segregated as white, green, or various hues of orange. The F_2 segregated fitted a 9:3:4 (white:green:orange) ratio in 2006 ($\chi^2 = 2.2$, $P = 0.33$), 2007 ($\chi^2 = 3.7$, $P = 0.16$) and pooled over years ($\chi^2 = 0.3$, $P = 0.86$), which is indicative of the action of two recessive epistatic loci (Table 4). These epistatic loci are as *A* and *B* herein, where *A_B_* individuals have white mesocarp, *aaB_* possess orange mesocarp, and *A_bb* and *aabb* genotypes develop fruits with green and orange mesocarp, respectively. If the orange-colored class is omitted, then F_2 individuals with white and green mesocarp color segregate to define the action of a single recessive locus that segregated in the observed 3 white to 1 green mesocarp fruit color ratio ($\chi^2 = 0.19$, $P = 0.66$). Segregation of orange, if white and green fruit mesocarp color are taken collectively as one class, fit a simple one locus model, which was also observed [3(non-orange):1(orange); $\chi^2 = 0.12$, $P = 0.73$]. The BC_1P_2 (*AaBb* × *aabb*) progeny segregated 1:1:2 [white (*AaBb*): green (*Aabb*): orange (*aaB_*)] for mesocarp fruit color in 2006. Likewise, if white and green mesocarp color groups are taken collectively in 2006 to form one class, segregation adequately fit a 1 (non-orange):1 (orange) ratio ($\chi^2 = 0.19$ $P = 0.67$). These segregation ratios (1:1:2 and 1:1), however, could not be fit using either 2007 data ($\chi^2 = 24.8$, $P = 0.000$, and $\chi^2 = 10.7$, $P = 0.001$, respectively) or when data were pooled over years ($\chi^2 = 21.1$, $P = 0.008$ and $\chi^2 = 7.0$, $P = 0.008$, respectively).

Genetic variance estimates

Variance component estimates (i.e., σ^2_A, σ^2_D, V_{AxD}, σ^2_G, σ^2_P, $\sigma^2_{P'}$, and σ^2_E) are presented in Table 5. Estimates of additive and dominance variances for QβC and FM were substantial and positive. However, the relative magnitude of effects for these traits

Table 4 Inheritance of fruit mesocarp color in melon (*Cucumis melo* L.) as obtained from segregating progeny derived from a cross between Chinese line 'Q 3-2-2' (P_1; white mesocarp) and 'Top Mark' (P_2; orange mesocarp) evaluated at Hancock, Wisc. in 2006 and 2007

Generation	Year	Phenotypic classes[a]			Segregation		
		WH[b]	GR[b]	ORG[b]	Test ratio	χ^2	*P*
F_2	2006	118	37	40	9:3:4	$\chi^2 = 2.2$	0.332
	2007	108	34	63	9:3:4	$\chi = 3.7$	0.160
	Total	226	71	103	9:3:4	$\chi^2 = 0.3$	0.857
BC_1P_1	2006	230	0	0	–	–	–
	2007	286	0	0	–	–	–
	Total	516	0	0	–	–	–
BC_1P_2	2006	73	55	135	1:1:2	$\chi^2 = 2.7$	0.266
	2007	79	35	169	1:1:2	$\chi^2 = 24.8$	0.000
	Total	152	90	304	1:1:2	$\chi^2 = 21.1$	0.000

[a] Phenotypic classes are based on the visual color categories where GR, WH, and ORG refer to green, white and orange mesocarp tissue, respectively

[b] Color grouping according to the English Royal Horticultural Society (RHS) Mini-color Chart (2005). *WH* white mesocarp color (RHS-155B or RHS-157B), *GR* green mesocarp color (RHS-145B) and *ORG* refer to light orange mesocarp color (RHS-18C), orange mesocarp color (RHS-23C), and orange-green mesocarp color (RHS-19B/RHS-149D)

varied depending on analysis type (i.e., GMA or VCA). The additive genetic variance for QβC was generally greater than the dominance variance when estimated by GMA. In contrast, estimates of dominance variance by VCA for QβC were greater than the additive genetic variance. Similarly, GMA for FM variation defined additive genetic variance as greater than the dominance variance. In contrast, additive variance for FM was less than dominance variance as estimated by VCA. Except for dominance variance of FM in GMA, estimated variance values for FM and QβC were at least double their standard errors in VCA and GMA.

Generation means analyses employed the use of joint scaling tests based on an additive-dominance model and sequential parameter model fitting. Data over years for FM did not adequately fit a simple additive-dominance three-parameter model, indicating a degree of epistatic control over these traits. Sequential model fitting suggests that homozygote × heterozygote interactions, heterozygote × heterozygote interactions, and additive genetic variances were important in fitting an epistatic model for FM ($\chi^2 = 2.14$; $P = 0.003$).

Heritability estimates

Broad-sense heritability estimates were relatively high (0.74–0.99 for QβC and 0.47–0.91 for FM) in both experiments (Table 5). Narrow-sense heritability was 0.55 for QβC and 0.62 for FM as estimated by GMA. Based on VCA of the individual plants variation within F_3 family, narrow-sense heritability estimates were 0.27 and 0.14 for QβC and FM, respectively. In contrast, narrow-sense heritabilities of QβC and FM were 0.68 and 0.57, respectively, when estimation was based on F_3 family mean variances.

Minimum number of effective factors

The minimum effective factors estimated via VCA were ~4 for the QβC and ~16 for the FM (Table 5).

Phenotypic and genotypic correlations

Phenotypic correlations between QβC and FM were not significant when estimated using BC_1P_2 progeny ($P = 0.19$). Nevertheless, relatively low positive phenotypic correlations were detected between QβC and FM ($P = 0.01$ and $r = 0.13$) when assessed using F_2 progeny data. Significant genetic correlations between QβC and FM were not detected in any population examined.

Discussion

The inheritance of flesh color and the accumulation of β-carotene

Clayberg (1992) observed that the segregation of mesocarp color fit a 12:3:1 (orange: white: green) in the F_2 progeny derived from Golden Beauty Casaba (white mesocarp) × green mesocarp line (derived from a cross of Crenshaw × Honeydew). This study suggested that mesocarp color in melon was controlled by dominant epistasis among two genes, white flesh (*wf*; Imam et al. 1972) and green flesh (*gf*; Hughes 1948). Recently, Monforte et al. (2004) observed a 50:25:9 and 32:19:8 (white:green:orange) mesocarp color segregation in an F_2 population and doubled haploid lines (DHL), respectively, that were derived from a cross between the Korean accession 'Shongwan Charmi' PI 161375 (green mesocarp) and 'Piel de Sapo' (white mesocarp). In that experiment, green mesocarp segregated as a single recessive locus if orange mesocarp phenotype was not included in the analysis [i.e., 3:1 and 1:1 (white: green) in F_2 progeny and DHL, respectively] as would be expected for the action of *gf*. However, segregation that included the orange mesocarp phenotype did not fit to any single/double-gene model, and, thus its inheritance must be considered independent of genes controlling white and green mesocarp. In contrast, mesocarp color segregation of RIL derived from the cross AR 5 (orange mesocarp) × 'Harukei No 3' (green mesocarp) (Fukino et al. 2008), and PI 16375 (green mesocarp) and 'Véndrantais' (orange mesocarp) (Périn et al. 2002) fit a single locus segregation model (1:1; orange: green), and as such mesocarp color is expected for the action of *wf*. The discrepancies between these studies are likely due to differences in parental constitution and the cross-specific genetic control conditioning the mesocarp-colored phenotype.

The genetic studies conducted herein sought to clarify the inheritance of mesocarp color variation in

Table 5 Genetic and environmental components of variance, heritabilities and standard error for β-carotene content in fresh fruit mesocarp tissue and fruit maturity in melon (*Cucumis melo* L.) assessed by generation means analysis of segregating progeny [F_1 ($n = 5$), F_2 ($n = 400$), BC_1P_1 ($n = 516$), and BC_1P_2 ($n = 546$)] and variance components analysis of F_3 families ($n = 116$) derived from a cross between Chinese line 'Q 3-2-2' (P_1) and 'Top Mark' (P_2) and evaluated at Hancock, Wisc. in 2006 and 2007

Genetic parameter[a]	Generation means analysis		Genetic parameter[c]	Variance components analysis	
	β-carotene (μg g^{-1})	Fruit maturity[b]		β-carotene (μg g^{-1})	Fruit maturity[b]
σ^2_A	4.61 ± 0.41	1.18 ± 0.11	σ^2_{F3}	1.67 ± 0.22	0.42 ± 0.06
σ^2_D	3.05 ± 1.08	0.24 ± 0.34	σ^2_A	1.17 ± 0.30	0.26 ± 0.09
$\sigma^2_{A\ x\ D}$	5.00 ± 0.31	0.18 ± 0.07	σ^2_D	2.00 ± 0.36	0.62 ± 0.18
σ^2_G	7.66 ± 1.15	1.42 ± 0.36	σ^2_P	2.14 ± 0.04	0.94 ± 0.02
σ^2_E	0.71 ± 1.00	0.48 ± 0.34	σ^2_{PF}	1.74 ± 0.22	0.48 ± 0.06
σ^2_P	8.37 ± 1.53	1.90 ± 0.50	h^2_{BP}	0.74 ± 0.16	0.47 ± 0.15
$\sigma^2_{P'}$	7.55 ± 0.27	2.25 ± 0.08	h^2_{BF}	0.99 ± 0.23	0.91 ± 0.30
h^2_B	0.92 ± 0.14	0.75 ± 0.19	h^2_{NP}	0.27 ± 0.07	0.14 ± 0.05
h^2_N	0.55 ± 0.05	0.62 ± 0.06	h^2_{NF}	0.68 ± 0.18	0.57 ± 0.19
			n	3.5	15.9

[a] σ^2_A, σ^2_D, $\sigma^2_{A\ x\ D}$, σ^2_G, σ^2_E, σ^2_P, $\sigma^2_{P'}$, h^2_B, h^2_N, and n are the additive genetic variance, dominance genetic variance, additive genetic variance component x dominance genetic component of variance interaction, genetic variance, environmental variance, phenotypic variance $= \sigma^2_A + \sigma^2_D + \sigma^2_E$, phenotypic variance $= 2\sigma^2_{F2}$, broad-sense heritability, and narrow-sense heritability, respectively

[b] Fruit maturity based on fruit maturity ranking (1–6), which refers to the 6 week harvesting period starting from the first mature fruit (full slip)

[c] $\sigma^2_{F3}, \sigma^2_A, \sigma^2_D, \sigma^2_P, \sigma^2_{PF}, h^2_{BP}, h^2_{BF}, h^2_{NP}, h^2_{NF}$, and n are the variance among F_3 families, additive genetic variance, dominance genetic variance, phenotypic variance of individual plants within F_3 families, phenotypic variance of F_3 family means, broad-sense heritability based on phenotypic variance of individual plants within F_3 families, broad-sense heritability based on phenotypic variance of F_3 family means, narrow-sense heritability based on phenotypic variance of individual plants within F_3 families, narrow-sense heritability based on phenotypic variance of F_3 family means, and the minimum number of effective factors, respectively

USWS melon (Group Cantalupensis). The genetic control of fruit mesocarp color in F_2 progeny was epistatically recessive (i.e., digenic 9:3:4; white: green: orange). Moreover, when green and white mesocarp were grouped into a single class (i.e. non-β-carotene), it was dominant to orange mesocarp (12:4; $\chi^2 = 0.12$ $P = 0.73$). Likewise, the segregation in BC_1P_2 progeny (2006; Table 4) fit a simple recessive locus when green and white mesocarp were grouped into a single class [1:1 (orange: non-orange) ratio]. Nevertheless, segregation ratio in BC_1P_2 in 2007, and data pooled over years show an excess of orange mesocarp phenotype. Since β-carotene accumulation in melon fruit is affected by environment (Cuevas et al. 2008), we hypothesize that green mesocarp genotypes may accumulate β-carotene. At low β-carotene concentrations, green mesocarp may appear to have a slight orange hue that could, in some instances, be misclassified as orange (e.g. ORGGR phenotypes; Fig. 1).

The segregation differences between the present study (Group Cantalupensis) and that of Monforte et al. (2004; Group Inodorus) are remarkable. For instance, herein phenotypes having a green mesocarp were relatively infrequent [71 of 400 total F_2 fruit (~18%); Table 4]. In contrast, Monforte et al. (2004) reported that individuals bearing fruit having orange mesocarp were relatively infrequent [9 of 65 total F_2 fruit (~14%)] in their study. In addition, while Monforte et al. (2004) concluded that the orange mesocarp segregation was independent from white and green mesocarp, the inheritance of the three color mesocarp groups (white, green and orange) are considered related as reported herein. The genetic distances between Group Cantalupensis and Group Indorus market types are appreciable, (Staub et al. 2000), and, thus, the genetic control of fruit mesocarp color among such market types may differ. In watermelon (*Citrullus* ssp; Henderson et al. 1998), three gene models with multiple allelic series, which

cause different types of epistatic interactions, have been used to explain the inheritance of mesocarp color.

Herein, we hypothesized a two-gene recessive epistatic model for the control of fruit mesocarp color in Group Cantalupensis USWS market types, where orange mesocarp segregates as single recessive locus if white and green mesocarp phenotypes are grouped into one color class (3:1; white/green:orange). Given that such a two-gene model can account for white, orange and green mesocarp color phenotypes, we predicted that RIL derived from this cross could be useful in resolving inconsistencies relating to the mesocarp color inheritance in melon. For instance, we hypothesize that true-breeding white mesocarp RIL (*AABB*) would yield progeny that would develop fruit possessing a white mesocarp when crossed to RIL possessing fruit with a green (*AAbb*) or orange (*aaBB* and *aabb*) mesocarp. Likewise, if RIL with green mesocarp were crossed with orange mesocarp resulting progeny could bear fruit with either a white (*AAbb* × *aaBB*) or green (*AAbb* × *aabb*) mesocarp. Moreover, the assessment of progeny derived from strategic intermating of DHL or RIL varying in interior fruit color described in other studies (Monforte et al. 2004; Fukino et al. 2008) and the RIL developed from the F_3 individuals described herein could further elucidate the inheritance of mesocarp color in melon.

The segregation within F_3 families (i.e., orange, green, and white fruit mesocarp), is suggestive of the interaction of more than two genes. Quantitative trait loci analysis employing F_3 families used herein identified three QTL associated with mesocarp color variation with putative epistatic interaction supporting this genetic model (Cuevas et al. 2009). Moreover, the two major QTL controlling mesocarp color (*β-carM.9.1*, LOD = 23.4, $R^2 = 40\%$; *β-carM.8.1*, LOD = 7.81, $R^2 = 11\%$) are located in regions that are syntenic with *wf* (Fukino et al. 2008; Périn et al. 2002) and *gf* gene (Monforte et al. 2004). Thus, it is likely that while the interaction of these two genes control much of the mesocarp color variation observed in Group Cantalupensis, their interaction with other minor color-controlling genes produce hues in each mesocarp color category. In fact, empirical estimates suggest that approximately four factors operate to control expression of β-carotene (i.e., non-orange and hues of orange) in the fruit of the cross-progeny examined herein (Table 5). The evaluation of RIL derived from a 'USDA 846-1' (orange mesocarp) × 'Top Mark' (orange mesocarp) mating identified five QTL associated with β-carotene content (i.e., orange color intensity) at Hancock, Wisc. in 2005 (Cuevas et al. 2008), where three QTL explained >10% of the variation associated with fruit β-carotene content. Genetic interactions between such QTL could produce the diversity of mesocarp fruit colors observed herein and support the contention that both major and minor genes operate to control the mesocarp color in the progeny examined.

Fruit maturity

The inheritance of FM must be considered complex and likely controlled by many genes with relatively small effects (Table 5). A three-parameter additive-dominance model (GMA) did not adequately explain the observed variation in FM, which suggests the influence of digenic or higher-order epistatic interactions in trait control. However, QTL analysis using F_3 families identified three QTL (Cuevas et al. 2009), which two have relatively large effects (FM6.1, LOD = 14.0, $R^2 = 35\%$; FM11.1, LOD = 8.5, $R^2 = 20\%$). This phenomenon has come to be known as the "Beavis effect", where QTL effects are biased upward when mapping population size is relatively small (~100 individuals) such that the capability to detect all QTL associated with a target trait (e.g., FM) is comparatively low (Beavis 1998). Although dominance variance for FM was not significant in GMA, significant dominant variance was detected in VCA, and thus must be considered in breeding programs that are interested in developing early maturing cultivars. The type and magnitude of epistatic interactions will likely determine the efficacy of ΔG in the derived F_3 and BC populations. Inbred line development that results in an increase in additive variance could facilitate the identification of unique genotypes (i.e., increased early FM with high Qβ C). Moreover, the fixation of alleles controlling FM could lead to increased utility of the additive variance (i.e., conversion of epistasis variance to additive variance) during germplasm improvement (Goodnight 1988). The initial fixation process of FM genes might, in fact, be enhanced by marker-assisted selection (MAS) using three previously identified QTL controlling FM (Cuevas et al. 2009).

The results reported herein (Table 5; VCA) are similar to those of Zalapa et al. (2006) who employed segregating RIL (USWS market type background) for the analysis of early flowering. Moreover, narrow-sense heritabilities estimates for FM calculated herein from F_2 and BC progeny were relatively high (GMA, $h^2_N = 0.62$; Table 5). In contrast, estimates based on individual F_3 plants (VCA) were comparatively low ($h^2_{NP} = 0.14$) to those based in F_3 family means ($h^2_{NF} = 0.57$). Given that ΔG is based on trait heritability (Bernardo 2002), greater predicted ΔG for FM will likely be made using family selection when compared to selection based on individual plants in this population. The genetic estimations and germplasm evaluation conducted herein, in fact, were used to select parents for hybrid analysis of line 'Q 3-2-2' × USWS germplasm (Luan et al. 2010).

The relatively high heritabilities, low dominance variance and significant additive variance for FM and QβC, as well the lack of correlation between these traits suggests that early generation (F_3 and BC), multi-location selection may result in substantial trait improvement (i.e., early yield and high QβC). The initial introgression and stabilization of β-carotene expression (i.e., orange mesocarp) can be achieved visually through phenotypic selection. However, the deployment of MAS for the early identification of genotypes with orange mesocarp may be cost effective (Cuevas et al. 2009). Moreover, enhancement of quantity of β-carotene (i.e., intensity of orange mesocarp color) may be achieved if significant amounts of the phenotypic variation are explained by QTL. Previous QTL analyses using RIL (derived from 'Top Mark' as a parent) evaluated at Hancock, Wisc. have identified useful QTL associated with yield components (Zalapa et al. 2007), fruit quality (Paris et al. 2008), and QβC in fruit (Cuevas et al. 2008). Thus, for the Group Cantalupensis population examined herein, MAS may be effective for increasing QβC and introgressing early FM genes, while retaining high yield and fruit quality.

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